VEGETATION DYNAMICS IN THE CENTENNIAL SANDHILLS, BEAVERHEAD COUNTY, MONTANA: DESCRIPTION AND MODEL WITH UTILITY FOR MANAGEMENT

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for
United States Department of Interior
Bureau of Land Management
State Office, Billings, Montana
Assistance Agreement No. 1422-E950-A1-0006
Task Order No. 36

This document should be cited as follows:

Lesica, P. and S. V. Cooper. 1996. Plant succession in the Centennial Sandhills of Beaverhead County, Montana: A description and model with utility for management. Montana Natural Heritage Program, Helena, MT. 28 pp.

Summary

The Centennial Sandhills support a mosaic of forb- and shrub-dominated vegetation in various stages of succession. Three rare to uncommon, seral plant communities (two early seral, one late seral) succeed to the late seral-climax *Artemisia tridentata* ssp. *tridentata/Festuca idahoensis* plant association, also noted as rare in Montana; additionally four rare plants occur only in early seral vegetation. Therefore, both early and late seral stages must be present on the landscape to protect biological diversity. Changes in disturbance regimes appear to be leading towards a loss of early seral vegetation, especially in areas of low topographic relief.

We sampled vegetation throughout the sandhills in lower slope erosion (blowout), upper slope deposition, and stabilized sites, estimating canopy cover of all vascular plant species and measuring soil organic matter and shrub ages. We ordinated our stands along a successional gradient using canonical correspondence analysis constrained by three environmental variables: total vegetation cover, litter cover, and soil organic matter. Early seral vegetation on lower slope erosion sites is dominated by *Chrysothamnus viscidiflorus* and *Stipa comata*, while *C. viscidiflorus*, *Agropyron dasystachyum* and *Psoralea tenuiflora* dominate early seral stands on upper slope deposition sites. Late seral vegetation is dominated by *Artemisia tridentata* ssp. *tridentata, Festuca idahoensis, Stipa comata* and *Lupinus sericeus*.

We used our empirically-derived successional sequences and information on the effects of the three principal disturbances: fire, ungulates and pocket gophers (*Thomomys talpoides*), taken from the literature to develop models of sandhills vegetation dynamics. These models suggest that fire followed by intense ungulate grazing may be the only way to restore early seral vegetation to areas of low topographic relief. In areas of high topographic relief, restoring presettlement fire frequency should be adequate to maintain pocket gopher habitat and thus a high proportion of early seral vegetation.

Introduction

The Centennial Sandhills in southwest Montana cover more than 8,000 acres and occur at the highest elevations of any sandhills ecosystem in the Northern Rocky Mountains. These sandhills support the occurrence of four rare to uncommon plant communities; the *Chrysothamnus viscidiflorus/Agropyron dasystachyum* (syn. *Elymus lanceolatus)/Psoralea tenuifolia* and *Chrysothamnus viscidiflorus/Stipa comata/Psoralea tenuifolia* early seral plant communities, the late seral *A. tridentata* ssp. *tridentata/Stipa comata,* and the late seral-climax *Artemisia tridentata* ssp. *tridentata/Festuca idahoensis* plant association. The sandhills also provide habitat for four rare plant species including two regional endemics, *Astragalus ceramicus* var. *apus* (painted milkvetch) and *Oenothera pallida* var. *idahoensis* (Idaho pale evening primrose)(Lackschewitz et al. 1984). *A. ceramicus* var. *apus* requires early seral open sand habitat to persist (Schassberger 1988), and the other three rare species may also be confined to this type of habitat.

Natural disturbance processes, such as fire and grazing, maintain many landscapes as mosaics of patches in different seral stages (Pickett and White 1985). The presence of all seral stages is important for maintaining the biological diversity of most landscapes (Bunnell 1995, Pickett and Thompson 1978). Many rare plants may require early successional habitat (Jacobson et al. 1991, Menges 1992, Parsons and Browne 1982); this is particularly true in sandhills habitat (Bowles et al. 1990, Hawkes and Menges 1995, Pavlik and Manning 1993, Schassberger 1988). Animals may also require the open nature of early seral sandhills vegetation (Ballinger and Watts 1995).

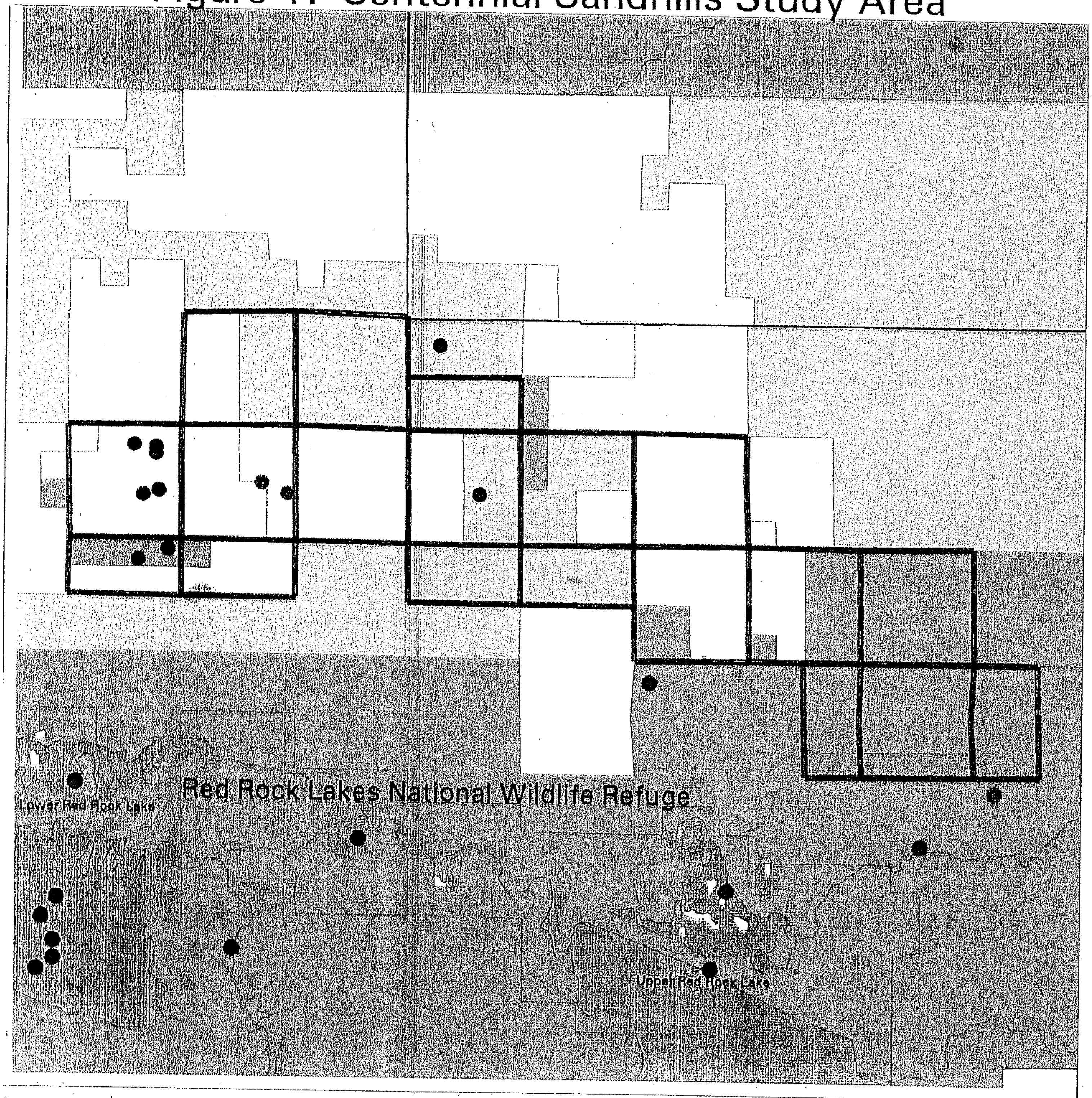
Fire, ungulate grazing and pocket gopher (*Thomomys talpoides*) activity are three important types of disturbance that play a role in shaping the vegetation dynamics in the Centennial Sandhills. The purpose of our study is to describe how sandhills vegetation changes through succession and then use this information, combined with our knowledge of how fire and grazing affect vegetation, to gain an understanding of how succession and these disturbances interact to affect composition. Our model of vegetation dynamics can be used to evaluate the effects of management activities on the vegetation patch mosaic and biological diversity in the Centennial Sandhills landscape.

Study site

The Centennial Sandhills occur in the northeast corner of the Centennial Valley, a broad trough at the head of the Red Rock River. The valley floor lies at 6,500-6,600 ft with the Centennial Mountains rising abruptly to ca. 10,000 ft on the south and grading more gently into the Gravelly and Snowcrest ranges on the north. Upper and Lower Red Rock Lakes are large, shallow, natural bodies of water at the east end of the valley. The Centennial Sandhills are found in a band 1-2 miles wide and ca. 9 miles long on the north side of the lakes (see Figure 1 with sandhill area outlined in black).

The sandhills are small, generally stabilized, dunes that formed from wind-blown sands deposited in the basins of Red Rock Lakes, probably during the late Pleistocene (ca. 10-12,000 BP). At this time with the waning of cold and pluvial climates the lakes retreated, exposing sandy shorelines. Shores furthest from the center of the lakes

Figure 1. Centennial Sandhills Study Area



Animals
Plants
Plant Communities
Other
County boundary
Centennial Sandhills Study Area
Streams
National Forests
National Wildlife Refuges
Bureau of Land Management - Public Lands
Department of Fish, Wildlife and Parks
Lakes & Reservoirs

This map is intended to be used as a general reference on the locations of biological features of special concern. For additional information on any of these locations, please contact:

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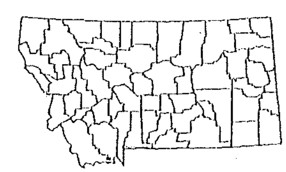

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would have been exposed first. Thus, dunes furthest from the lake may be the oldest (Olson 1958). Dune activity in this region is controlled by the tension between wind and vegetation cover. Periods of active movement have probably alternated with periods of relative stabilization. Periods of drought or disturbances such as fire or grazing may initiate new episodes of migration (Seevers et al. 1975). During periods of active migration the dunes move in accordance with prevailing winds from southwest to northeast, depositing a layer of sand on the gently sloping, broad valley floor. As sand is lost the dunes become smaller. Eventually enough sand is lost that vegetation stabilizes the dune, and movement ceases (Chadwick and Dalke 1965).

The interaction between vegetation and wind-blown sand controls dune morphology (Smith 1942). Examination of aerial photos of the area indicates that primary dunes are longitudinal (sensu Hack 1941), with low ridges running southwest-northeast, parallel to the direction of prevailing winds. Superimposed on these older ridges are blowout or parabolic dunes (sensu Hack 1941) that are ellipsoidal to elongate U-shaped and 30-60 ft high. Leward slopes are steep (ca. 30-60% slope), while windward slopes are more gently sloping and often bowl-, crater-, or trough-shaped. Prevailing winds of sufficient strength transport sand from the windward slope and deposit it on the leeward shoulder and/or slope, often in an "apron" around the blowout (Chadwick and Dalke 1965, Melton 1940, Smith 1965). In this way dunes move to the northeast. Shapes of individual dunes are modified from parabolic by strong cross winds and differential growth of stabilizing vegetation. Sand dunes in the Centennial Valley are in various states of activity. In general, the highest and most active dunes are in the western portion, north of Lower Red Rock Lake. Those in the eastern portion of the area are lower and well stabilized.

Livestock grazing has been the only significant human-caused disturbance affecting the Centennial Sandhills for which there is historical evidence; the advent of European-man in this valley has undoubtedly altered fire regimes, but on a local scale the alteration of this process is unknown . Pasturing of domestic sheep in the Centennial Valley began in the late 1800's, ostensibly in the centennial year 1876 thus giving rise to the valley's name, and continued until the 1940's. Cattle grazing replaced sheep pasturing and continues until the present. Permanent ranches were present in the valley during the first half of this century, and livestock grazing was likely higher at that time. Land managed by the BLM has been consistently grazed since 1939.

Four plant species considered rare in Montana occur in the Centennial Sandhills (Lesica and Shelly 1991). *Astragalus ceramicus* var. *apus* (G4T3-S1) and *Oenothera pallida* var. *idahoensis* (G5T4Q-S1) occur only in the Centennial Sandhills and the sandhills of southeastern Idaho. *Cryptantha fendleri* (G4-S1) is sparsely distributed throughout much of western North America, but is known from only two locations in Montana. *Elymus flavescens* (G4-S1) occurs in sandy soil in the northwest U.S., but in Montana occurs only in the Centennial Sandhills. In addition, three relatively unique plant communities occur in the Sandhills. Potential natural vegetation of the well-stabilized portions appears to be predominantly *Artemisia tridentata* ssp. *tridentata/Festuca idahoensis*, a plant association whose degree of rarity is designated by The Nature Conservancy as G3G4/S? (Bourgeron and Engelking 1994), indicating knowledge of its existence in the state to be only circumstantial. The Sandhills expression of this

type may require a phase designation to recognize the high canopy cover of *Stipa comata* (not described as typical of this c.t. in other locations). The most xeric sites support small patches of *A. tridentata* ssp. *tridentata/Stipa comata*, a putative c.t., possibly seral to *A. tridentata* ssp. *tridentata/F. idahoensis* and not described elsewhere in the western U.S. Early seral c.ts. identified based on limited sampling and ostensibly unique to this vicinity have previously been termed *Chrysothamnus viscidiflorus/Stipa comata* (G?/S?) and *Agropyron dasystachyum/ Phacelia hastata* (G2?/S2?, Cooper et al. 1995); with the additional sampling conducted in this study these communities might more appropriately be designated *C. viscidiflorus/S. comata/Psoralea tenuifolia* and *C. viscidiflorus/A. dasystachyum/Psoralea tenuifolia* (as they are in this report) to recognize the relative importance of the shrub component in these lightly vegetated communities.

Methods

Field methods Preliminary reconnaissance revealed that sites in the study area could be placed into three classes based on topography and the apparent status of sand movement: (1) lower slope erosion (blowouts), (2) upper slope deposition, and (3) stabilized on both upper and lower slopes. We used USGS topographic maps to circumscribe the sandhills area and then randomly selected a location in each section (1 square-mile) for sampling. At each of the 12 locations we sampled one stand representative of each of the three site classes. Of the sampled total of 40 stands (13 erosion, 13 deposition, and 14 stabilized) subjected to vegetation analysis, 35 were sampled on July 9-14, 1996 and these plots included the collection of soils information. The 5 additional plots were the product of extensive southwestern Montana field sampling in 1994 and recorded just floristic and non-soils site information; these plots were used for comparison purposes.

We sampled stands that appeared homogeneous in vegetation composition and structure (Mueller-Dombois and Ellenberg 1974). Efforts were made to sample areas where slope and aspect were constant; however, this was not always possible due to the relatively small scale of topographic changes in the sandhills.

Sample plots were circular with a 11.4 m radius. In some cases we had to modify the shape of our plot in order to accommodate the shape of stands. We employed Daubenmire's (1959) concept of canopy cover in estimating species abundance. Canopy cover of bare soil, rock, litter, moss and lichens, total shrubs, total graminoids and total forbs, was estimated to the nearest 10% Below 5%, was divided into two classes: 3% and 1%. Estimates of canopy cover were always made by the same investigator to minimize variation. We sampled the 35 stands on 9-14 July 1995.

Pocket gophers (*Thomomys talpoides*) activity was detected by the presence of diggings and mounds in the plots. Some sites were inferred to have been pocket gopher occupied from the subsequent badger diggings.

We collected three 10-cm cylindrical soil cores from randomly located points along a diameter in each plot. The three samples from each plot were combined, stored in paper bags and returned to the laboratory for analysis.

We collected at least three ground-level, stem cross sections from dominant shrubs in each plot. Species of *Artemisia* were sampled preferentially; however, *Chrysothamnus nauseosus* plants were sampled when *Artemisia* spp. were rare or absent. We estimated shrub age by counting annual growth rings at 10 X magnification following the caveats of Ferguson (1964).

Soil texture and organic matter are thought to be correlated with successional age in sandhills systems (Olson 1958). We analyzed ten randomly chosen samples for percent organic matter by the Wakley-Black method and for particle size distribution using the Bouyoucos technique. There was a strong correlation between percent organic matter and both percent sand ($r=-0.86$) and percent silt ($r=0.92$), indicating that percent organic matter and texture provide equivalent information. Consequently we chose percent organic matter to represent soil successional age and analyzed the remaining samples accordingly.

Vascular plant nomenclature generally follows Hitchcock and Cronquist (1973). *Koeleria cristata* is considered an illegitimate name. We have chosen to follow Wilken (1993) in calling it *Koeleria macrantha* (Ledeb.) J.A. Shultes.

Data analysis. Upper slopes and crests of sandhills often support different vegetation than the lower slopes and intervening swales (Barnes et al. 1984, Chadwick and Dalke 1965, Keeler et al. 1980). Thus we ordinated upper and lower slope stands separately using Canonical Correspondence Analysis (CCA; Palmer 1993, ter Braak 1986). CCA is succinctly defined as a method of direct ordination with the resulting ordination representing the variability of the environmental data as well as the variability of the species/plot data. The resulting ordination diagram thus expresses not only the pattern of stand (plot) and species compositional variation but also demonstrates the principal relationships between the stands and each of the environmental variables. Ordination in species space was constrained by regression on three site variables: percent bare soil, percent organic matter, and total canopy cover. In both the lower and upper slope seres we assumed that vegetation proceeds from the least productive (most bare soil, least organic matter, and least total canopy cover) to most productive as the dunes become increasingly stabilized (Billings 1941, Cowles 1899, Chadwick and Dalke 1965). This procedure ensures that the first axis of the ordination corresponds to a successional gradient. Only species present in at least five stands in the sere were used in this analysis. We used axis 1 scores determined by linear combination of variables to place stands in a putative seral sequence (Palmer 1993). Species scores along this axis were used to delineate important successional changes in species composition.

We tested the distinctness of early and late successional vegetation between the two seres with Multi-response Permutation Procedures (MRPP; Mielke 1984). MRPP provides a nonparametric multivariate test of the hypothesis of no difference between two groups based on a matrix of Euclidean differences. The probability value expresses the likelihood of finding a difference as, or more, extreme than the observed difference between groups based on all possible partitions of the data set. The 5-7 stands with the lowest and highest CCA axis 1 scores in each sere were used in the MRPP analysis and to compile constancy-coverage tables to describe early and late successional vegetation respectively.

Analyses were performed on a microcomputer using PC-ORD (McCune and Mefford 1995).

Results

Early successional upper slope and lower slope sites support different vegetation. Deposition areas on upper slopes had a sparse shrub cover of *Artemisia tridentata* ssp. *tridentata*, *Chrysothamnus viscidiflorus*, and *Tetradymia canescens* and a sparse ground layer of mainly *Agropyron dasystachyum* and *Psoralea tenuiflora*. Erosion sites (blowouts) on lower slopes had a sparse shrub cover of mainly *C. viscidiflorus* and a ground layer dominated by *Stipa comata, A. dasystachyum, P. tenuiflora* and *Machaeranthera canescens* (Table 1). Results of the MRPP analysis indicate that these two groups of stands are different ($t=-3.44$, $P=0.004$). As succession proceeds

Table 1. Mean percent canopy cover (Cov.) and frequency (Freq.) of common ($\geq 1\%$) vascular plant species in lower slope erosion, upper slope deposition and stabilized stands.

	Lower erosion (7)		Upper depos. (6)		Stabilized (11)	
	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.
Shrubs						
Artemisia tridentata ssp. *tridentata*	0.9	0.83	3.0	0.67	14.3	1.00
Artemisia tripartita	--	--	--	--	5.8	0.45
Chrysothamnus nauseosus	1.1	0.86	2.5	0.67	0.2	0.27
Chrysothamnus viscidiflorus	4.0	1.00	3.2	1.00	0.7	0.55
Leptodactylon pungens	1.0	1.00	1.2	0.83	0.4	0.36
Tetradymia canescens	1.1	0.86	4.5	0.83	0.6	0.27
Grasses						
Agropyron dasystachyum	5.0	1.00	18.8	1.00	4.4	1.00
Festuca idahoensis	0.4	0.43	0.3	0.33	11.6	0.91
Koeleria macrantha	0.3	0.29	0.3	0.33	4.5	0.91
Oryzopsis hymenoides	1.0	1.00	1.3	1.00	--	--
Poa nevadensis	2.3	1.00	1.2	0.83	3.1	0.82
Stipa comata	9.1	1.00	3.0	0.83	35.7	1.00
Forbs						
Agoseris glauca	0.4	0.43	1.0	0.67	0.5	0.45
Allium textile	1.5	0.71	1.2	0.83	0.1	0.09
Artemisia dracunculus	0.3	0.29	1.0	0.67	0.4	0.18
Chaenactis douglasii	1.1	0.86	1.3	1.00	0.1	0.09
Comandra umbellata	1.3	1.00	1.3	0.67	0.4	0.36
Cryptantha fendleri	0.4	0.43	1.0	1.00	--	--
Descurainia richardsonii	1.0	1.00	1.3	0.67	0.3	0.27
Eriogonum ovalifolium	1.9	1.00	1.5	0.83	0.2	0.18
Eriogonum umbellatum	0.6	0.57	0.5	0.50	1.3	0.73
Linum perenne	1.3	1.00	1.0	1.00	--	--
Lithospermum ruderale	0.1	0.14	0.3	0.17	1.1	0.27
Lupinus argenteus	1.0	0.71	2.5	0.67	0.5	0.36
Lupinus sericeus	--	--	--	--	11.0	0.82
Machaeranthera canescens	3.4	1.00	0.7	0.67	0.3	0.27
Mertensia oblongifolia	0.1	0.14	0.2	0.17	1.3	0.73
Opuntia fragilis	1.1	0.86	0.5	0.50	0.7	0.55
Phacelia hastata	2.4	1.00	2.7	1.00	0.6	0.55
Phlox longifolia	1.1	0.86	0.7	0.67	0.9	0.72
Psoralea tenuiflora	3.6	0.86	11.0	1.00	1.0	0.18
Viola nuttallii	--	--	--	--	1.5	0.73
Totals						
Total shrub	5.3		11.2		22.2	
Total grass	12.4		20.0		56.7	
Total forbs	12.0		18.3		16.7	
Litter (percent cover)	0.8		1.4		77.5	
Organic matter (percent)	0.3		0.6		1.8	

the two early seral disturbance types converge toward a single late seral vegetation dominated by *Artemisia tridentata* ssp. *tridentata* (or *A. tripartita*), *Festuca idahoensis, S. comata*, and *Lupinus sericeus* (Table 1). MRPP analysis indicates that stabilized stands in the two seres are similar at the 5% level (t=-1.63, P=0.07).

Figures 2 (lower slope/swale sere) and 3 (upper slope sere) convey the results of canonical correspondence analysis (CCA, axis 1 versus 2); (only Fig. 2 has centers of species importance plotted and only for a limited number of ecological importance, those showing marked cover change with succession). CCA was performed for the continuous variables percent total organic matter, total vegetal cover and bare ground; the open boxes or solid circles represent individual plots, the stars indicate centers of species importance and the dotted arrows represent each environmental variable plotted in the direction of maximal change across the diagram. The length of the arrow is proportional to the magnitude of change in that direction; the longer a particular variable's arrow the greater its correlation with community variation. A point corresponding to an individual plot (or species) can be related to each environmental vector by drawing a perpendicular from the plot to the vector. The order in which plots (species) are projected onto the arrow is a measure of their position in relation to the environmental factor. Plots with their perpendicular projections at or near the arrow's tip will be positively correlated with the environmental factor.

CCA performed well at displaying the primary successional pathways for both lower slope/swale (Fig. 2) and upper slope (Fig. 3) seres. The two seres are quite comparable; for both there was a strong correlation between stand scores based on species composition and those based on % bare soil, % organic matter and % total canopy cover ($r \geq 0.93$). The lower slope/swale sere was characterized by increases in *Artemisia tridentata* ssp. *tridentata, Festuca idahoensis, Koeleria macrantha*, and *Mertensia oblongifolia* and decreases in *Oryzopsis hymenoides, Linum perenne*, and *Psoralea tenuiflora* (Fig. 2). The upper slope sere was similar, but *Agropyron dasystachyum* rather than *O. hymenoides* was a prominant decreaser.

Stem cross sections were obtained from 75 *Artemisia tridentata* ssp. *tridentata*, 9 *A. tripartita*, and 16 *Chrysothamnus nauseosus*, ranging in estimated age from 7 to 71 years (Table 2). While *A. tridentata* must establish from seed, *A. tripartita* and *C. nauseosus* are able to sprout from root crowns following fire (Hironaka et al. 1983). Thus, stand age estimates based on the latter two species will tend to be higher than those based on *A. tridentata*. Furthermore, light surface burns increase exposed soil and may decrease organic matter without killing all shrubs. Examples of light surface burns are represented by stands 06 and 34 (Fig. 2) whose positions in regard to the vectors appears anomolous because exposed substrate has been increased beyond that predicted by their stand ages. Nonetheless, stand age based on age of the oldest shrub was strongly correlated with CCA axis 1 scores for both upper slope ($r=0.66$, $P<0.01$) and lower slope/swale ($r=0.55$, $P=0.03$) seres, confirming the validity of CCA axis 1 as a successional ordination.

The average and range in values for percent organic matter content of the upper 10 cm of the soil profile is for stabilized, depositional and erosional positions, respectively, 1.76 (0.87-3.39), 0.68 (.05-1.18, and 0.56 (.26-

1.61). Percent bare ground differs markedly between stabilized sites (average = 15%, range 02-47) and disturbed conditions, depositional (ave. = 82%, range 22-98) and erosional sites (ave.= 92%, range 80-98).

Pocket gopher diggings were observed in both deposition (64%) and erosion (30%) sites and were more frequent on slopes. Evidence of pocket gophers was not observed in late seral (stabilized) stands.

Table 2. Sample plot listing of selected site and biotic variables, including associated disturbance status (erosional, depositional, stabilized).

Sample Site Designation	Seral Status	Stand Age	Sand %	Silt %	Clay %	Texture	% Organic Matter	% Bare Ground
SC001	S[1]	24TR[2]	84	10	06	loamy sand	1.66	27[3]
SC002	E	32CN	--	--	--	--	0.26	92
SC003	E	36CN	--	--	--	--	0.26	92
SC004	S	26TR	--	--	--	--	1.80	10
SC005	D	23CN	89	06	05	sand/loamy sand	0.59	92
SC006	S	71TT	--	--	--	--	1.22	12
SC007	D	14TT	--	--	--	--	0.37	85
SC008	E	13TT	--	--	--	--	1.23	85
SC009	S	42TT	86	09	05	loamy sand	1.57	03
SC010	E	14TT	--	--	--	--	0.44	92
SC011	S	36TT	--	--	--	--	1.53	30
SC012	E	12TT	--	--	--	--	0.42	92
SC013	D	15TT	90	05	05	sand	0.58	92
SC014	D	none	--	--	--	--	0.05	98
SC015	S	37TT	--	--	--	--	1.32	47
SC016	E	18TT	--	--	--	--	0.41	92
SC017	D→S	42TT	86	07	07	loamy sand	1.18	22
SC018	E	23TT	--	--	--	--	0.32	92
SC019	D	16TT	--	--	--	--	1.18	92
SC020	S	34TT	--	--	--	--	1.67	25
SC021	E	33TT	90	04	06	sand/loamy sand	0.34	98
SC022	D	38TT	--	--	--	--	0.68	92
SC023	S	52TT	--	--	--	--	3.39	05
SC024	D	13TT	--	--	--	--	0.56	92
SC025	E	14TT	89	06	05	sand/loamy sand	0.45	98
SC026	D	32TT	--	--	--	--	0.71	92
SC027	S	48TT	--	--	--	--	1.57	10
SC028	E	39CN	--	--	--	--	0.41	98
SC029	D	42CN	85	08	07	loamy sand	0.71	68
SC030	S	41TR	--	--	--	--	1.41	
SC031	S	37TT	--	--	--	--	0.87	03
SC032	S	44TR	--	--	--	--	2.27	02
SC033	D	17TT	91	05	04	sand	0.86	75
SC034	E→S	44TT	--	--	--	--	1.61	80
SC035	S	56TT	81	12	07	loamy sand	2.61	03

[1] S = stabilized sites, E = erosional positions, D = depositional positions, → = manifestly transitional
[2] Species of oldest stem sectioned, TR= *Artemisia tripartita*, TT= *Artemisia tridentata* ssp. *tridentata*, CN= *Chrysothamnus nauseosus*
[3] Midpoint of cover class

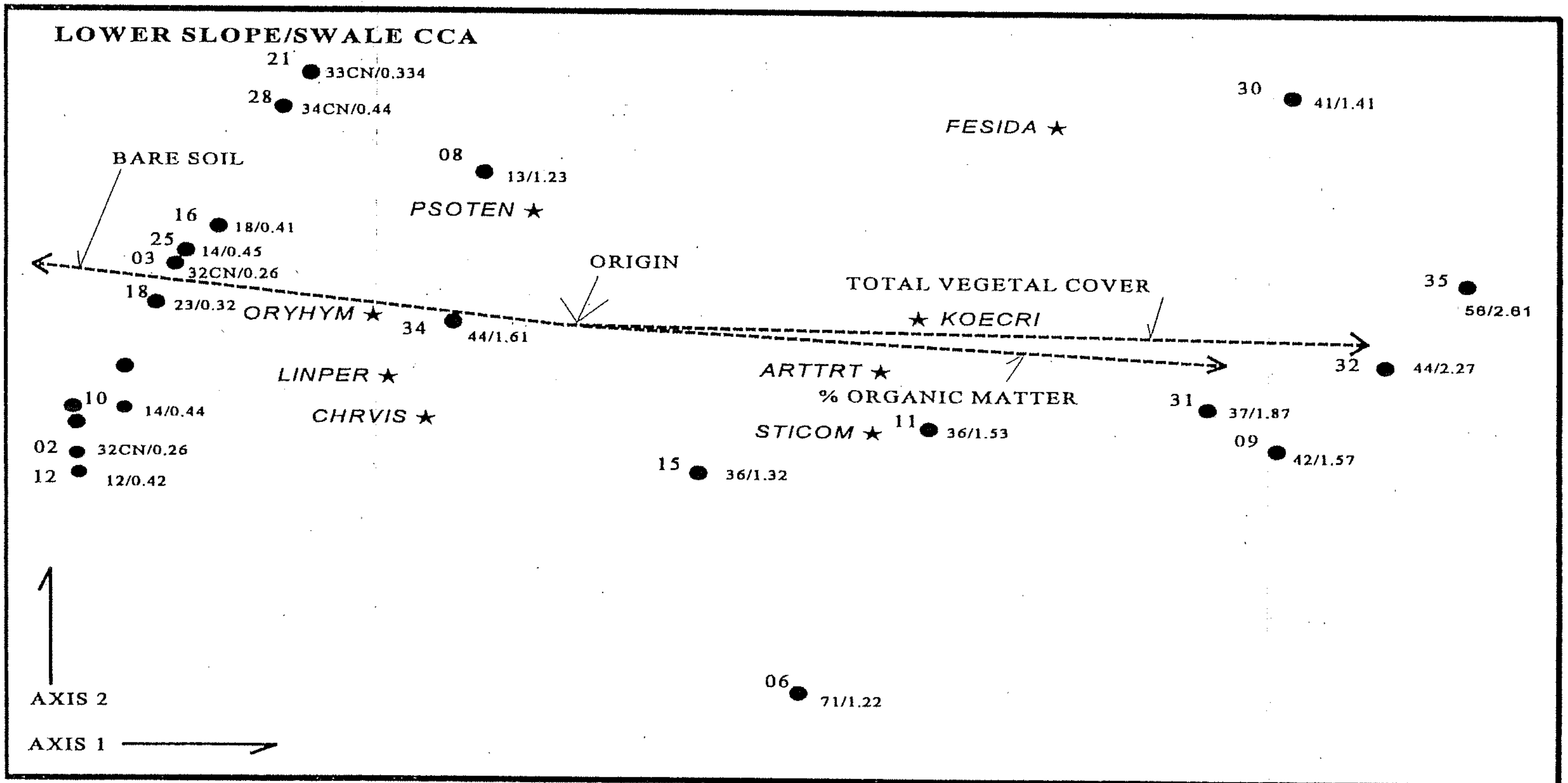

Figure 2. Canonical correspondence analysis diagram indicating location of sample plots of lower-slope/swale position (erosional) in environmental space defined by axis 1 and 2 and representing bare soil, percent organic matter and total vegetal cover. Plot numbers to left of open boxes with stand age (based on oldest sectioned stem) and percent organic matter to the right of slash. Species representative early-seral and late-seral stages are plotted to show their positions relative to gradients of the contraining variables. Individual species can be related to specific variables by projecting a perpendicular from the species to the variable's vector. The order in which the species project to the vector from the tip downward is an indication of the declining strength of association of the variable and species (see text for expanded explanation; ★ indicates center of species importance; *ARTTRI* = *Artemisia tridentata* ssp. *tridentata*, *CHRVIS* = *Chrysothamnus viscidiflorus*, *FESIDA* = *Festuca idahoensis*, *LINPER* = *Linum perenne*, *ORYHYM* = *Oryzopsis hymenoides*, *PSOTEN* = *Psoralea tenuiflora*).

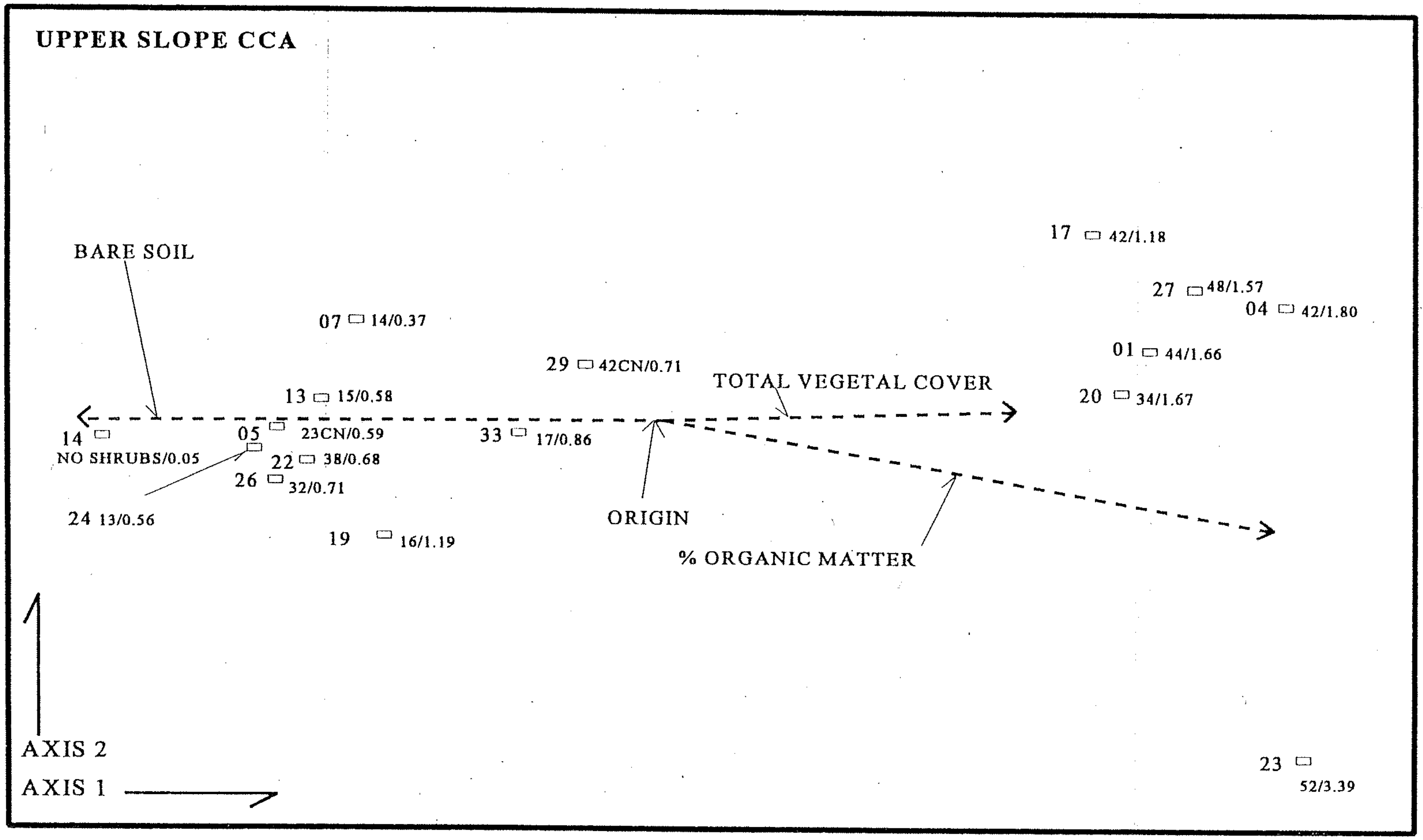

Figure 3. Canonical correspondence analysis diagram showing location of sample plots of upslope positions (depositional) sere in environmental space defined by axes 1 and 2 and representing bare soil, percent organic matter and total vegetal cover. Plot numbers are placed to left of open boxes with stand age (based on oldest sectioned stem, CN for *Chrysothamnus nauseosus*, undesignated for *Artemisia tridentata* ssp. *tridentata*) and percent organic matter to the right (separated by slash). Relative length of hatched arrows indicates strength of that variable in explaining variance of the sample plot distribution.

Rare plants were exclusively associated with early successional habitats. *Astragalus ceramicus* var. *apus* was found in 45% of lower slope erosion stands but was absent from upper slope deposition and stabilized sites ($\chi^2 = 7.0$, $P = 0.008$). On the other hand, *Cryptantha fendleri* was more common in deposition sites (83%) compared to only 36% of erosion stands ($\chi^2 = 5.3$, $P = 0.02$). *Oenothera pallida* var. *idahoensis* occurred in both erosion and deposition stands with low frequency. *Elymus flavescens* was rare and was observed only in reconnaissance, occurring on very active deposition sites.

Discussion

We used multi-response permutation procedures (MRPP) to determine that early successional vegetation of upper slope deposition and lower slope erosion sites was different, although late seral, stabilized vegetation was similar regardless of topographic position. We then employed canonical correspondence analysis to describe prominent vegetation changes that occur during succession in both seres. We now use this knowledge of primary successional pathways and vegetation responses to disturbance to construct models of sandhills vegetation dynamics.

Succession. Succession along the lower slope/swale sere occurs as the gently sloping to level, lower portions of blowouts are gradually invaded by the vegetation of the adjacent steppe community. Active erosion surfaces support a sparse shrub canopy dominated by *Chrysothamnus viscidiflorus*, *Tetradymia canescens* and a sparse cover of *Stipa comata* and *Agropyon dasystachyum*. Scattered perennial forbs such as *Psoralea tenuiflora*, *Linum perenne, Phacelia hastata, Allium textile, Chaenactis douglasii* and *Machaeranthera canescens* also occur. As succession proceeds *C. viscidiflorus, T. canescens* and most of the early-seral, common forbs decrease while *Artemisia tridentata* ssp. *tridentata* (or *A. tripartita*), *Festuca idahoensis, Koeleria macrantha, Lupinus sericeus* and *Mertensia oblongifolia* increase. As plants invade and cover increases, less sand is moved over the dune by the wind (Malakouti et al. 1978).

Succession on the upper slopes occurs when the deposition of sand decreases on crests and lee slopes. Plants no longer suffer annual burial, and colonization proceeds at a more rapid pace. Early successional stands have a sparse to moderate shrub cover of *Artemisia tridentata* ssp. tridentata, Tetradymia canescens, *Chrysothamnus viscidiflorus* and *Artemisia tripartita*. *Agropyron dasystachyum* is the common grass. *Psoralea tenuiflora* is the only consistently abundant forb, but *Comandra umbellata, Phacelia hastata* and *Eriogonum ovalifolium* may be common. As succession proceeds these forbs decrease while *Festuca idahoensis, Koeleria macrantha* and two different forbs, *Lupinus sericeus* and *Viola nuttallii* increase. Late successional stands are similar to those in lower slope positions.

Succession is retarded, and climax communities revert to earlier seral stages when vegetal cover is removed and wind erosion is reinitiated. Three processes cause an increase in bare ground in sandhills systems: fire, ungulate grazing, and pocket gopher digging and grazing (Bragg 1978, Pfeiffer and Steuter 1994, Potvin and Harrison 1984,

Steuter et al. 1995, Wolf 1973). In addition to these three factors, extended periods of drought cause a reduction in vegetation and an increase in open ground and erosion potential (Weaver 1954, Weaver and Albertson 1936).

It is instructive to compare the percent organic matter of Centennial Sandhills sites (Table 2) with values found by Munn et al. (1978) for typical southwestern Montana range habitat types in a late seral to climax condition. For a typical soil catena ranging from warm, dry *Stipa comata/Bouteloua gracilis* to cold, moist *Festuca idahoensis-Agropryon caninum* they reported A1 horizon percent organic matter values ranging from 2.8 to 10.2 %, with a typical *Artemisia tridentata/Festuca idahoensis* stand at 4.8 %. The fact that percent organic matter values of Centennial Sandhills sites (Table 2), even for the putatively oldest ones (most of which are climax in *A. tridentata* ssp. *tridentata/Festuca idahoensis*) are at least 1.5 percentage points lower than those of Munn et al. (1978) argues for even our stabilized stands being 1) still relatively immature, not yet at a soil-vegetation equilibrium, 2) developed on instrinically less productive sites which in turn produce less litter and incorporated organic matter, 3) developed on sandy soils which are known to retain less organic matter as a fossil record (Cannon and Nielsen 1984), or 4) some combination of the three aforenamed factors.

Comparing *F. idahoensis* and *A. tridentata* ssp. *tridentata* average cover values, 12 and 14% respectively, for our stabilized sites with those values found in southwestern Montana studies by Husby (1982) for late-seral *A. tridentata* ssp. *vaseyana/Festuca idahoensis* h.t. (43 and 35 % respectively) and greater western Montana (38 and 20 % respectively) by Mueggler and Stewart (1980) shows our sites to be relatively low in cover and thus production and amount of organic matter incorporated into the soil column. This comparison does not permit the separation of temporal effects from those related to site differences but clearly shows that Centennial Valley sites are not the same, compositionally or in terms of site parameters, as late seral representatives of the closely allied *A. tridentata* ssp. *vaseyana/Festuca idahoensis* h.t. of greater western Montana.

Fire. Average fire-return intervals at the ecotone between forest and sagebrush grasslands of the high valleys in southwest Montana were 25-50 years prior to European settlement (Arno and Gruell 1983, Houston 1973, Wright et al. 1979), and fire frequency was likely higher in the grasslands proper (Arno and Gruell 1983). These fires cause a mosaic of severely to lightly burned patches and reduced the cover of *Artemisia tridentata* which is easily killed by fire and often requires in excess of ten years to reestablish preburn stature and density (Blaisdell 1953, Mueggler and Blaisdell 1958, Harniss and Murray 1973). Early seral dominant shrubs, *Chrysothamnus* spp. and *Tetradymia canescens*, resprout immediately following fire (Blaisdell 1953, Mueggler and Blaisdell 1958, Young and Evans 1978) and may increase in abundance (Harniss and Murray 1973, Wright et al. 1979). Reconnaissance of the Centennial Sandhills revealed extensive burned areas that lacked *Artemisia* spp. shrubs; however, deeply dished, burned stumps of large shrubs at or below ground level indicate that *A. tridentata* was once present.

The rhizomatous, early seral dominants *Agropyron dasystachyum* and *Psoralea tenuiflora* will suffer little damage from fire (Wright et al. 1979), whereas dominant late seral grasses, *Festuca idahoensis* and *Stipa comata*, are often harmed by fire (Wright and Klemmedson 1965, Wright et al. 1979) and may not return to preburn levels for 12-30+ years (Harniss and Murray 1973). Furthermore, early seral vegetation is relatively sparse and would not be likely to carry a hot fire.

Fire suppression and the concomitant increase in vegetal cover is thought to be the main cause of dune stabilization in the Nebraska Sandhills in the recent past (Wolf 1973). In these sandhills, vegetation cover was reduced for 1-2 years following fire (Bragg 1978), and regrowth tended to be more retarded on dunes compared to lower slope and interdune locations (Wolf 1973). Fire may cause an increase in the proportion of rhizomatous grasses compared to the bunchgrasses, possibly resulting in destabilization of dune vegetation because bunch grasses are more effective at deterring wind erosion (Pfeiffer and Steuter 1994).

Artemisia tripartita is the dominant late seral shrub in portions at the west end of the study area. This species is capable of surviving fire by resprouting from the root crown (Hironaka et al. 1983, Daubenmire 1970). Succession should proceed more quickly following fire in areas dominated by *A. tripartita* comapared to those dominated by *A. tridentata* ssp. *tridentata*. We expect less early seral vegetation in these areas when fire frequencies are equal.

Pocket gophers. Pocket gopher (*Thomomys talpoides*) diggings in the Centennial Sandhills were observed in early successional vegetation of both upper slope depositional (58%) and lower slope erosion (45%) sites and were more frequent on steeper slopes. Evidence of gophers was not observed in late seral plots. Pocket gophers reduce vegetal cover and increase bare soil by grazing vegetation and mounding soil (Foster and Steubendieck 1980), and are reported to create mounds more frequently in open areas and on slopes (Ellison 1946). Pocket gopher activity is noted to increase in disturbed areas, most particularly those areas experiencing heavy grazing, because forbs are favored over grasses and sedges (Mielke 1977). Over twenty times more soil was moved by *Geomys bursarius* in a moderately over-grazed area characterized by more forbs and weedy species than was moved in good condition tallgrass prairie on the same site (Beuchner 1942).

In montane meadows, pocket gophers (*Thomomys*) prefer to eat forbs, especially those with fleshy roots, although grasses are also eaten (Ellison and Aldous 1952, Tryon 1947, Ward and Keith 1962). In a Colorado shortgrass prairie, a habitat similar in species composition to the Centennial Sandhills, pocket gophers preferred *Opuntia polyacantha* and *Stipa comata*; *Agropyron smithii* and *Psoralea tenuiflora* were also used but not preferred (Vaughan 1967). In this dry habitat with few succulent roots, *Opuntia* provided an important source of moisture (Vaughan 1967). Pocket gophers had a diet composed mainly of *O. polyacantha* pads and roots and *Agropyron smithii* leaves in sagebrush and grass steppe in Beaverhead County (Cotter 1963).

Although pocket gophers preferentially consume forbs in montane meadows and semi-arid grasslands, recruitment of these plants may be enhanced on the bare soil of mounds (Martinsen et al. 1990). Rhizomatous

grasses and forbs generally increase with pocket gopher grazing and digging (Cotter 1963, Ellison and Aldous 1952). In southwestern Montana Cotter (1963) documented extensive postburn areas colonized by pocket gophers and described a successional sequence similar to that of the Sandhills in that forbs and seral shrubs (*Ceratoides lanata*) are early-sere dominants of gopher-disturbed sites.

Pocket gophers retard or reverse succession by increasing open sand, often eliminating vegetation in small patches, and causing a relative increase in the rhizomatous species *A. dasystachyum* and *Psoralea tenuiflora* at the expense of bunchgrasses such as *S. comata* and *F. idahoensis*. Gophers may prefer early and mid-seral vegetation because their principal foods, *A. dasystachyum, Psoralea tenuiflora*, and *Opuntia fragilis* are most common. Pocket gophers are likely an important force in preventing early to mid-seral habitats from advancing to late successional vegetation by reinitiating blowouts.

Pocket gopher abundance will be influenced by the amount of mid- and early seral vegetation. Disease and badger predation may also be important in controlling gopher density on a local scale (individual blowouts) and allowing successional processes to be reinitiated..

Ungulates. Bison (*Bison bison*) were present in the Centennial Valley prior to the advent of Europeans in southwest Montana (Haines 1955). Since settlement the study area has been grazed by sheep and cattle. In general, cattle prefer grasses while sheep prefer forbs, although there is a great deal of variability among different sites and different populations of animals (Mueggler and Stewart 1980). Both *Agropyron dasystachyum* and *Stipa comata* are given fair or fair-to-good palatability ratings. *Festuca idahoensis* is rated as good to very good for both grazing species. Palatability of *Psoralea tenuiflora* is very poor and poor for cattle and sheep respectively (Mueggler and Stewart 1980). Livestock are expected to retard succession, mainly by reducing vegetal cover from grazing and creating open sand from trampling on steep slopes. There is little evidence that moderate stocking levels result in an increase of early successional habitat (Schassberger 1988).

Drought Soils supporting seral communities have lower water-holding capacity because they have less organic matter and coarser texture. Slope and hilltop positions will suffer the highest evaporation stress (Tolstead 1942). Consequently, the adverse effects of prolonged drought will be most pronounced in early seral sandhills communities, lowering vegetal cover and increasing instability. More xeric conditions will occur on southerly slopes due to increased evapotranspiration resulting from higher solar radiation loads and exposure to prevailing winds (Lotspeich and Smith 1953).

Interactions Moderate to heavy livestock grazing will decrease the likelihood of fire by decreasing the density of fine fuels (Arno and Gruell 1986). However, livestock and other ungulates prefer the new growth following fire, and fire followed by moderate to heavy grazing may destabilize sandhills vegetation more than the sum of two disturbances separately. Fire and large ungulate grazing had a greater combined effect at reducing vegetal cover in the Nebraska sandhills than either alone (Bragg 1978). Together fire and grazing reduce bunchgrasses more than rhizomatous grasses (Pfeiffer and Steuter 1994).

There is little overlap between the diets of plains pocket gophers (*Geomys bursarius*) and bison in the Nebraska sandhills (Steuter et al. 1995). The principle effect of both livestock and pocket gophers is to retard succession by increasing the abundance of open sand. We expect the effects of livestock and pocket gophers would be additive.

Pocket gophers may depend on fire to create new habitat in the Centennial Sandhills. Gophers occur only in early and mid-seral communities, and fire is the only disturbance that removes shrub cover and converts late seral vegetation to potential gopher habitat. Prolonged drought would exacerbate the effects of grazing but would lower the likelihood of fire by reduction in fuels.

<u>The model.</u> We have shown that early seral vegetation of lower slopes (blowouts) is significantly different than that on upper slopes (deposition areas), but late seral vegetation is similar in the two habitats. Two models are needed to describe the vegetation dynamics of the sandhills ecosystem; however, the models are similar. Large scale increases in early seral vegetation can occur only when lower slope vegetation is destabilized and blowouts are initiated. Consequently, the lower slope model will be most critical for making management decisions. Here we present verbal and graphical representations of lower slope sandhills vegetation dynamics (Fig. 4) followed by a brief description of how the upper slope model differs (Fig. 5).

Succession. In the absence of disturbance, early seral vegetation, dominated by *Chrysothamnus viscidiflorus* and *Stipa comata,* has low shrub (5%), grass (10%) and litter (1%) cover. Late seral vegetation is dominated by *Artemisia tridentata* ssp. *tridentata* (or *A. tripartita*), *Stipa comata, Festuca idahoensis*, and *Lupinus sericeus*. Shrub cover (22%) is moderate, and grass (57%) and litter (77%) cover are high. Mid-seral vegetation is intermediate in composition. Succession proceeds more slowly on the larger, steeper hills because they are exposed to higher wind speeds. Succession will be retarded during periods of drought and advanced under moist conditions that favor recruitment and growth of vegetation. Succession will also be advanced in areas where *A. tripartita* is dominant.

Fire. Fire causes late seral vegetation to revert to mid-seral. Mid- and early seral vegetation have too little litter or shrub cover to carry a fire. Prolonged drought reduces fuel and makes fire less likely and less severe.

Ungulate grazing. Moderate grazing probably has little effect except for localized trampling that may help maintain mid-seral vegetation.

Pocket gophers. Gopher digging and grazing is rare in late seral vegetation and converts mid-seral to early seral vegetation, promoting blowouts on a local scale. Gopher populations are likely highest in early seral stages and in a posititive feedback loop their grazing/burrowing tends to maintain this favorable seral condition.

Fire + ungulate grazing. Fire followed by grazing can initiate blowouts and convert late seral to early seral vegetation.

Drought. Prolonged drought retards succession by reducing standing crop biomass and being differentially stressful to potential site dominants such as *Festuca idahoensis*.

The upper slope model (Fig. 5) differs in the following ways: (1) early seral vegetation has higher shrub (11%) and grass (20%) cover, (2) mid-seral vegetation may have sufficient fuel to carry a light fire, (3) Fire followed by moderate to heavy ungulate grazing will cause mid-seral vegetation to revert to early seral, (4) fire followed by gopher digging and grazing will also cause mid-seral vegetation to revert to early seral.

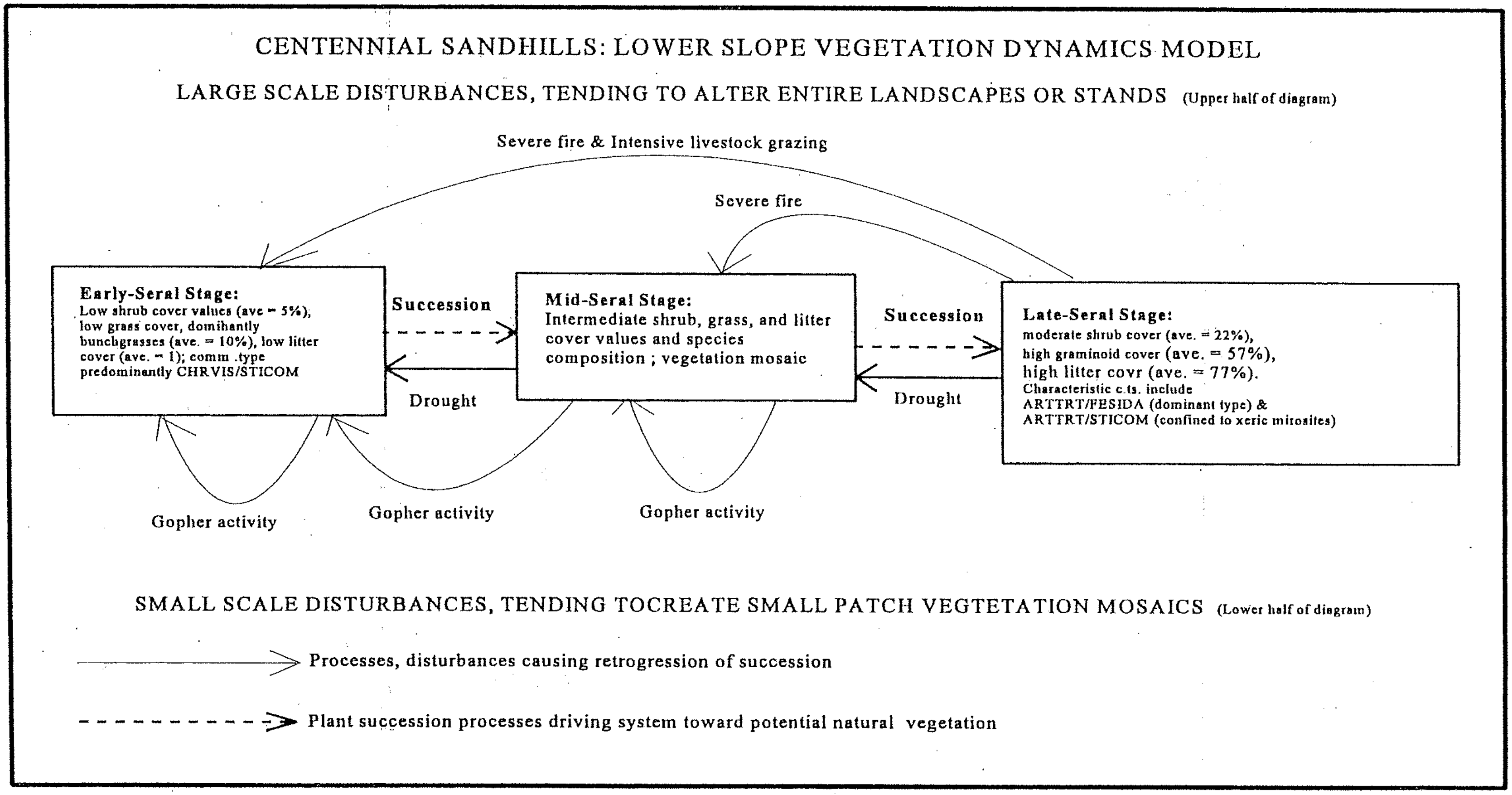

Figure 4. Box-and-arrow model of successional processes and seral stages for lower slope/swale positions within the Centennial Sandhills landscape. Solid arrows denote processes, disturbances likely to retard or cause retrogession when applied to existing stages of vegetation structure and composition; hatched arrows indicate complex of successional processes driving system toward a late-seral or dynamically and long-term stable state (see text for further explanation).

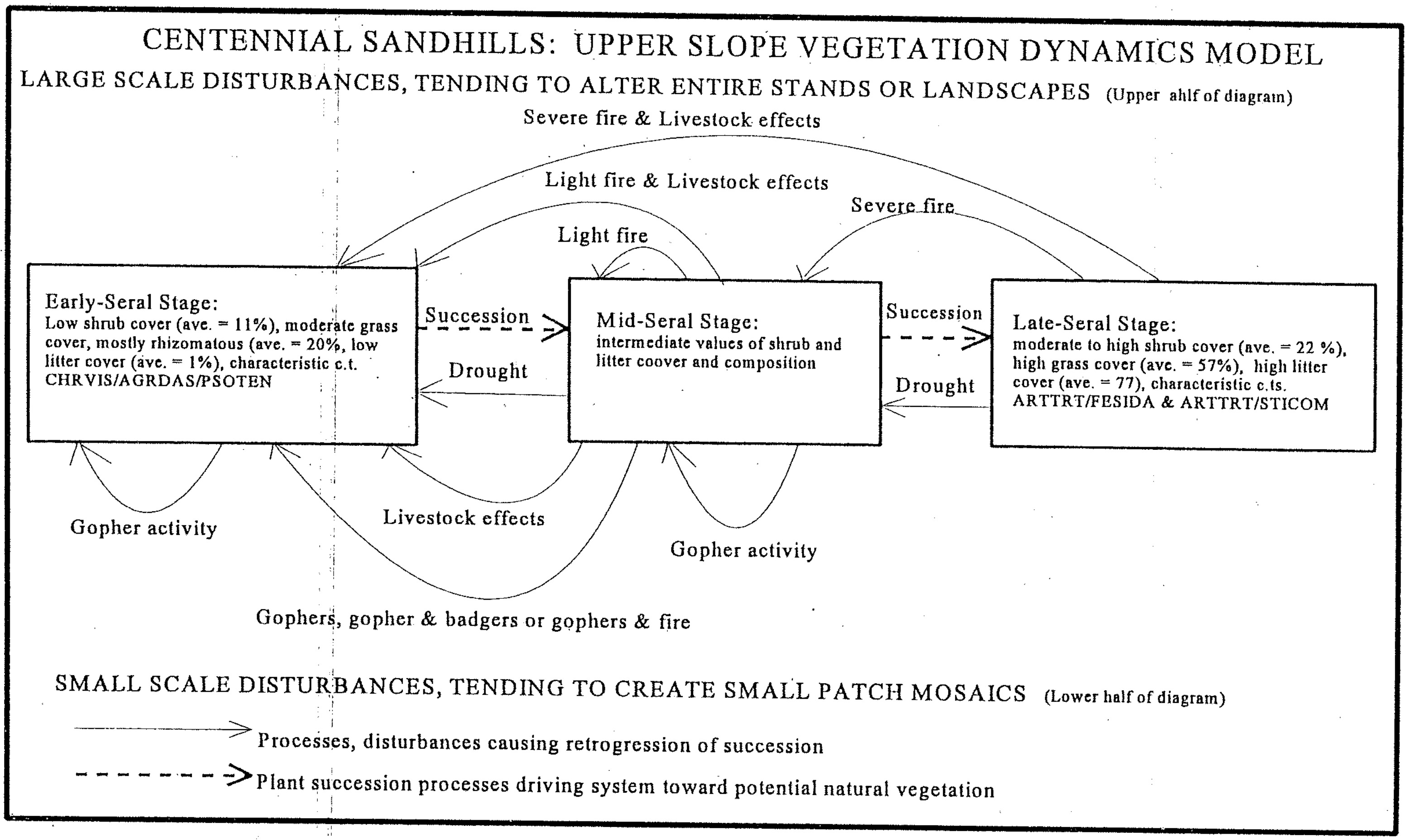

Figure 5. Box-and-arrow model of successional processes and seral stages for upper slope positions within the Centennial Sandhills landscape. Solid arrows denote processes, disturbances retarding or causing retrogression when applied to exiting stages of vegetation structure and composition. Hatched arrows indicate complex of successional processes driving system toward a late seral or dynamically, long-term stable state (see text for additional explanation).

Implications for Management

Maintaining the biological diversity of the Centennial Sandhills depends on maintaining a mosaic of different seral vegetation types. The four rare plants, *Astragalus ceramicus* var. *apus, Oenothera pallida* var. *idahoensis, Cryptantha fendleri* and *Elymus flavescens,* all require the open sand of early seral vegetation to persist. A faunal inventory of the Centennial Sandhills has not been done; however, it is likely that some animals, especially small predators, will also require open sand habitat (Ballinger and Watts 1995). For example, *Cicindela formosa,* a predaceous tiger beetle, was common in early seral, lower slope blowouts but was not observed elsewhere. Late seral to climax vegetation of the Centennial Sandhills is also unique, and includes *Artemisia tridentata* ssp. *tridentata/Festuca idahoensis* and *A. tridentata* ssp. *tridentata/ Stipa comata,* plant associations not reported elsewhere in Montana and which may harbor rare or unusual organisms.

Disturbance regimes in the Centennial Sandhills have likely been altered significantly. Man-caused fire suppression has been effective at reducing the frequency of wild fires in Montana over the past 50-60 years (S. Arno, pers. com.). Although there have been fires in the Centennial Sandhills during this time, it is likely that fire-return intervals have become longer. The intensity of grazing by bison in pre-European times is not known, although many parts of southern Beaverhead County were heavily impacted (Lesica and Cooper, manuscript in preparation). We suspect that livestock densities (mainly sheep) were high, and grazing was season long in the late 1800's and the early 1900's. Livestock grazing on public lands in the sandhills has probably been more moderate in the past 50 years. Lower fire frequencies and moderate stocking rates have probably resulted in a decrease in early seral vegetation compared to presettlement conditions.

The height and frequency of sandhills varies across the study area, probably in relation to distance from the original source of sand (Chadwick and Dalke 1965). More level areas may be less likely to have active blowouts, and would be expected to have higher proportions of late seral vegetation. Nonetheless, active sandhills can form on level terrain if vegetation is not aggressive (Smith 1965). Existing topography as well as disturbance regimes control the proportion of seral vegetation on the Centennial Sandhills landscape.

Much of the eastern portion of the sandhills, including Red Rock Lakes Wilderness, has lower topographic relief and is almost completely dominated by mid- to late seral vegetation. Pocket gophers were uncommon, probably due in part to the paucity of slope habitat. Only *Cryptantha fendleri* of the four rare plant species was observed in this area. Controlled fire followed by intense livestock grazing for 1-2 years should significantly reduce vegetal cover, allow reinitiation of active blowouts, and ultimately increase the proportion of early seral vegetation. Returning to presettlement fire return intervals of 20-30 years and moderate ungulate grazing, at least in years following burns, will probably maintain a significant proportion of early seral vegetation.

There is more topographic relief in the western third of the sandhills. Active blowouts, early seral vegetation, and pocket gophers are common. All four rare plants are present, although *Elymus flavescens* is

uncommon. Gopher activity is an important force in initiating blowouts and maintaining early seral vegetation in this area. Managing for presettlement fire return intervals of 20-30 years should increase the proportion of mid-seral vegetation, thereby increasing pocket gopher habitat. Increased gopher activity will increase the proportion of early seral vegetation. High levels of ungulate grazing will also help maintain early seral vegetation on slopes where trampling is significant. Fire followed by high levels of ungulate grazing could destabilize a significant proportion of the late and mid-seral vegetation on the hills.

The above scenarios are based on our successional models and should be viewed as hypotheses rather than predictions. We strongly suggest testing these hypotheses using demonstration areas where various management strategies are applied on a small scale with or (if necessary) without replication.

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***** APPENDIX A *****

CENTENNIAL SANDHILLS CONSTANCY/COVERAGE TABLE WITH MINIMUM-MAXIMUM RANGE AND INCLUDING ALL SPECIES

POSITION/SERAL STAGE DESIGNATION

Species Abbreviations	STABLILIZED N = 13	DEPOSITIONAL* N = 11	EROSIONAL∇ N = 11
***** Shrubs *****			
AMEALN	0 (0) [0- 0]	9 (1) [1- 1]	0 (0) [0- 0]
ARTFRI	0 (0) [0- 0]	9 (1) [1- 1]	18 (1) [1- 1]
ARTTRP	31 (16) [3-20]	18 (1) [1- 1]	0 (0) [0- 0]
ARTTST	100 (13) [1-30]	73 (7) [1-20]	82 (2) [1-10]
CHRNAU	31 (2) [1- 3]	73 (3) [1-10]	82 (1) [1- 3]
CHRVIS	54 (1) [1- 3]	100 (3) [1-10]	100 (3) [1-20]
LEPPUN	31 (1) [1- 1]	73 (1) [1- 3]	100 (1) [1- 1]
ROSWOO	0 (0) [0- 0]	9 (1) [1- 1]	0 (0) [0- 0]
ROSWOOD	8 (1) [1- 1]	0 (0) [0- 0]	9 (1) [1- 1]
TETCAN	15 (2) [1- 3]	82 (5) [1-10]	64 (1) [1- 3]
***** Graminoids *****			
AGRCAN	8 (3) [3- 3]	0 (0) [0- 0]	0 (0) [0- 0]
AGRDAS	92 (4) [1-10]	100 (15) [3-60]	100 (5) [1-10]
BROTEC	0 (0) [0- 0]	9 (10) [10-10]	0 (0) [0- 0]
CALMON	23 (1) [1- 1]	46 (1) [1- 3]	73 (1) [1- 1]
CARDOU	8 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
CAREX	0 (0) [0- 0]	0 (0) [0- 0]	9 (1) [1- 1]
CARFIL	15 (1) [1- 1]	0 (0) [0- 0]	9 (1) [1- 1]
CARPEN	0 (0) [0- 0]	0 (0) [0- 0]	9 (1) [1- 1]
CARROI	15 (2) [1- 3]	0 (0) [0- 0]	0 (0) [0- 0]
CARROS	8 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
FESIDA	92 (11) [1-40]	27 (1) [1- 1]	36 (1) [1- 1]
FESOCT	8 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
KOECRI	100 (5) [1-20]	46 (1) [1- 1]	27 (1) [1- 1]
ORYHYM	0 (0) [0- 0]	73 (2) [1- 3]	82 (1) [1- 1]
POANEV	92 (4) [1-20]	82 (1) [1- 3]	100 (2) [1-10]
POAPRA	15 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
STICOM	100 (39) [3-80]	91 (11) [1-30]	100 (13) [1-40]
STIPAX	0 (0) [0- 0]	9 (1) [1- 1]	0 (0) [0- 0]
***** Forbs *****			
ACHMIL	23 (1) [1- 1]	9 (1) [1- 1]	0 (0) [0- 0]
AGOGLA	39 (1) [1- 1]	55 (1) [1- 3]	46 (2) [1- 3]
ALLTEX	15 (1) [1- 1]	64 (2) [1- 3]	64 (3) [1- 3]
ALYALY	0 (0) [0- 0]	0 (0) [0- 0]	9 (1) [1- 1]
ALYDES	0 (0) [0- 0]	18 (1) [1- 1]	0 (0) [0- 0]
ANTDIM	31 (1) [1- 1]	18 (1) [1- 1]	73 (1) [1- 3]
ANTMIC	8 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
ARAHIR	8 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
ARAHOL	8 (1) [1- 1]	27 (1) [1- 1]	36 (1) [1- 1]
ARTDOU	8 (3) [3- 3]	9 (1) [1- 1]	9 (1) [1- 1]
ARTDRA	15 (2) [1- 3]	64 (2) [1- 3]	27 (1) [1- 1]
ASTCER	0 (0) [0- 0]	0 (0) [0- 0]	46 (1) [1- 1]
ASTMIS	15 (1) [1- 1]	18 (1) [1- 1]	27 (1) [1- 1]
ASTSCO	0 (0) [0- 0]	0 (0) [0- 0]	9 (1) [1- 1]
BESWYO	8 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
CAMMIC	8 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
CHADOU	15 (1) [1- 1]	82 (1) [1- 3]	73 (1) [1- 3]
CHEFRE	8 (1) [1- 1]	18 (1) [1- 1]	9 (1) [1- 1]
CHELEP	46 (1) [1- 1]	91 (1) [1- 1]	64 (1) [1- 1]
CHENOP	0 (0) [0- 0]	9 (1) [1- 1]	0 (0) [0- 0]
COMUMB	46 (1) [1- 1]	55 (2) [1- 3]	82 (1) [1- 3]
CREACU	8 (1) [1- 1]	9 (1) [1- 1]	0 (0) [0- 0]
CRYFEN	0 (0) [0- 0]	91 (1) [1- 3]	36 (1) [1- 1]
DELGLA	0 (0) [0- 0]	9 (1) [1- 1]	0 (0) [0- 0]
DELNUT	8 (1) [1- 1]	0 (0) [0- 0]	9 (1) [1- 1]
DESRIC	39 (1) [1- 1]	73 (2) [1- 3]	82 (1) [1- 1]
DESRVR	0 (0) [0- 0]	9 (1) [1- 1]	0 (0) [0- 0]

* Depositional is equivalent to upper slope position
∇ Erosional is equivalent to lower slope/swale position

***** APPENDIX A (continued) *****

Species Abbreviations	*STABLILIZED N = 13	*DEPOSITIONAL N = 11	*EROSIONAL N = 11
***** Forbs *****			
DESSOP	8 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
DRANEM	8 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
EQUHYE	8 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
EQUVAR	23 (1) [1- 1]	9 (1) [1- 1]	9 (1) [1- 1]
ERICER	0 (0) [0- 0]	9 (1) [1- 1]	9 (1) [1- 1]
ERIGER	0 (0) [0- 0]	9 (1) [1- 1]	0 (0) [0- 0]
ERIHER	8 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
ERIOVA	31 (1) [1- 1]	91 (1) [1- 3]	82 (2) [1- 3]
ERIOVO	0 (0) [0- 0]	0 (0) [0- 0]	9 (1) [1- 1]
ERIUMB	77 (1) [1- 3]	64 (2) [1- 3]	55 (1) [1- 1]
ERYREP	23 (1) [1- 1]	18 (1) [1- 1]	0 (0) [0- 0]
FRIATR	0 (0) [0- 0]	9 (1) [1- 1]	0 (0) [0- 0]
GAYDIF	85 (1) [1- 3]	73 (2) [1-10]	46 (1) [1- 1]
LAPRED	31 (1) [1- 1]	64 (1) [1- 1]	55 (1) [1- 1]
LEPVIR	0 (0) [0- 0]	9 (1) [1- 1]	0 (0) [0- 0]
LINPER	8 (1) [1- 1]	73 (1) [1- 1]	82 (1) [1- 3]
LITRUD	23 (4) [1-10]	18 (2) [1- 2]	18 (1) [1- 1]
LOMTRI	15 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
LUPARG	46 (3) [1-10]	73 (3) [1-10]	64 (2) [1- 3]
LUPSER	69 (13) [1-20]	0 (0) [0- 0]	0 (0) [0- 0]
LYGJUN	0 (0) [0- 0]	9 (1) [1- 1]	0 (0) [0- 0]
MACCAN	31 (1) [1- 1]	82 (1) [1- 3]	91 (3) [1-10]
MEROBL	62 (2) [1- 3]	18 (2) [1- 3]	18 (1) [1- 1]
OENPAL	0 (0) [0- 0]	9 (1) [1- 1]	18 (1) [1- 1]
OPUFRA	54 (1) [1- 3]	73 (1) [1- 3]	91 (3) [1-10]
OROBAN	0 (0) [0- 0]	18 (1) [1- 1]	0 (0) [0- 0]
OROFAS	0 (0) [0- 0]	0 (0) [0- 0]	9 (1) [1- 1]
PENPRO	8 (1) [1- 1]	0 (0) [0- 0]	0 (0) [0- 0]
PHAHAS	62 (1) [1- 1]	100 (2) [1- 3]	100 (2) [1- 3]
PHLHOO	77 (1) [1- 3]	18 (1) [1- 1]	36 (1) [1- 1]
PHLLON	62 (1) [1- 3]	73 (1) [1- 1]	82 (1) [1- 3]
POLDOU	23 (2) [1- 3]	27 (1) [1- 1]	18 (1) [1- 1]
PSOTEN	8 (1) [1- 1]	100 (12) [1-30]	91 (5) [1-10]
TARLAE	23 (1) [1- 1]	18 (1) [1- 1]	0 (0) [0- 0]
TAROFF	39 (1) [1- 1]	9 (1) [1- 1]	9 (1) [1- 1]
TRADES	0 (0) [0- 0]	9 (1) [1- 1]	9 (1) [1- 1]
TRADUB	15 (1) [1- 1]	46 (1) [1- 1]	18 (1) [1- 1]
VIONUT	62 (2) [1- 3]	0 (0) [0- 0]	0 (0) [0- 0]